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Effects of water temperature, rearing temperature and population on swimming performance and temperature preference in Atlantic salmon (Salmo salar)

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Abstract

Understanding how animals respond to environmental temperatures is important for the survival and reintroduction of species. My objectives were to determine how swim performance responds across water temperatures, and how rearing temperature or population would affect this performance and temperature preference. Juvenile Atlantic salmon (*Salmo salar*) from two populations that are currently used for stocking in Lake Ontario (LaHave, Sebago) were reared at two temperatures (11°C, 19°C). I measured critical swim speed and burst swim speed across eight water temperatures (11 – 25°C). Water temperature had no effect on burst speed, while critical swim speed increased with increased temperatures. I found no effect of rearing temperature on burst speed, but critical swim speed was significantly higher for fish reared at 11°C than fish reared at 19°C. Temperature preferences aligned with rearing temperature in the Sebago population but not the LaHave population. Atlantic salmon demonstrate plasticity in swim performance and temperature preference.

Keywords

temperature, thermal performance curves, plasticity, genetic adaptation, burst speed, critical swim speed, temperature preference, shuttlebox, salmon

Co-Authorship Statement

All work was completed under the supervision of Bryan Neff at The University of Western Ontario. Glenn Tattersall from Brock University helped with study design, equipment set-up and analysis. Nicole Zathey performed data collection, analysis and wrote this thesis. The data contained in the thesis will be submitted for publication with Bryan Neff and Glenn Tattersall as co-authors.

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List of Abbreviations

SMR	standard metabolic rate
MMR	maximum metabolic rate
TPC	thermal performance curve
T_{opt}	optimal temperature
T_{crit}	critical temperature
ATP	adenosine triphosphate
OMNRF	Ontario Ministry of Natural Resources and Forestry
SD	standard deviation
n	sample size
LAH	LaHave population
SEB	Sebago population
CT_{max}	critical thermal maxima

Introduction

1.1 Thermal ecology

The effect of temperature on organismal fitness is currently a subject of major interest in the field of biology. These effects often differ between endotherms, which are organisms such as mammals or birds that can internally regulate their body temperature, and ectotherms, which are organisms such as insects, amphibians, and lizards that cannot internally regulate their body temperature. Since body temperature in ectotherms is dependent on environmental temperatures, understanding the relationship between temperature and fitness is of particular interest for ectotherms. Understanding how environmental temperatures will affect organism survival is important because temperature affects the distribution of species and speciation (Chen et al. 2011; Keller and Seehausen 2012; Hanly et al. 2017; Kong et al. 2017).

Three ways organisms can respond to temperature change are through genetic adaptation, phenotypic plasticity, or behaviourally by migrating to areas with a preferred temperature. Genetic adaptations are changes in the genotypes of populations that occur through natural selection and confer a fitness advantage (Fuller et al. 2010). Phenotypic plasticity is the ability of individuals of a particular genotype to change their phenotype in different environments (Pigliucci 2005). In some cases, both genes and environment can shape thermal performance, but this interaction is not well understood (Pigliucci 2005). Another way organisms can respond to environmental temperatures is through behavioural changes, such as moving to areas of preferred temperatures.

There is currently a gap in thermal ecology to better understand how organisms will respond to changing temperatures. It is not well understood the roles genetic adaptation or phenotypic plasticity will play in allowing organisms to survive in current thermal environments or persist as thermal environments change (Gunderson & Stillman 2015). My thesis will address this gap by looking at the effects of temperature on swim performance and temperature preference, and examining if these traits display plasticity or differ across populations in Atlantic salmon (*Salmo salar*).

1.2 The effect of temperature on physiology and evolution

Temperature has been labeled the "ecological master factor" in ectotherms because it affects many different aspects of an organism's life (Brett 1971). For ectotherms, temperature can affect growth, aerobic scope, and even drive speciation. Temperature plays an important role in growth because it increases metabolism by changing the rate of biochemical reactions associated with the breakdown and absorption of food products (Gillooly et al. 2001). Increased temperature can cause increases in enzyme activity that are important for metabolism, however, exposure to high temperatures can lead to enzymes becoming inactive or denaturing (Peterson et al. 2007).

Temperature also affects aerobic scope. Aerobic scope is the difference between standard metabolic rate (SMR, energy required to keep an organism alive when not feeding, reproducing or moving) and maximum metabolic rate (MMR) (Fry 1947; Farrell 2009). This difference gives an organism the capacity to perform aerobic activities (Casselman et al. 2012). As temperatures increase, kinetic energy in molecules increase, which leads to an increase in chemical reactions. As these reaction rates increase, the

resting metabolic rate and the need for oxygen to fuel metabolism increases. Over intermediate temperatures, MMR increases faster than SMR, leading to a large aerobic scope (Pörtner 2010). However, at higher temperatures MMR plateaus as the body is constrained by an upper level of metabolism and oxygen consumption, but SMR keeps increasing exponentially, until the two rates equal each other and aerobic scope collapses.

In addition to affecting growth and aerobic scope, temperature has been found to drive speciation in plants and animals across thermal environments. In 16 species of plants and animals, divergent selection based on thermal adaptations was linked to partial reproductive isolation, which can further lead to speciation (Keller and Seehausen 2012). In China, plant speciation rate was correlated with changes in historic temperatures as assessed by chloroplast and nuclear DNA (Kong et al. 2017). Therefore, temperature is one of the major ecological factors that affect ectotherms.

Many studies look at how acclimation temperature affects physiology or ecology. Acclimation involves the physiological response of an organism to its environment, and is often used on the short-term scale (weeks to months). For my thesis, I used the term rearing temperature instead of acclimation temperature because my fish were exposed to these temperatures throughout a time of growth and development (juvenile stage).

1.3 Thermal performance curves

Because temperature is such an important factor affecting ectotherms, there is significant interest in understanding how temperature can affect organismal fitness. One method for understanding this relationship is by using thermal performance curves (TPCs), which describe the effects of temperature on the relative performance of an organism over a

range of temperatures (Huey and Stevenson 1979). The classic shape for a TPC of an ectotherm is a left-skewed bell-shape, which initially shows a gradual increase in performance with increasing temperature, followed by a steep decline in performance at high temperatures (Huey and Stevenson 1979; Fig. 1). Two key measures that can be derived from TPCs are the optimal temperature (T_{opt}) and upper critical temperature (T_{crit}). T_{opt} is the temperature at which an individual's performance is maximized and T_{crit} is the upper temperature where performance falls to zero (Huey and Stevenson 1979). TPCs are believed to follow a bell-shape curve in part due to the relationship between temperature and aerobic scope, and traits linked to aerobic metabolism may thus be most likely to show this characteristic shape. Aerobic activities include growing and reproduction, which have direct links to fitness, which is the ability of an organism to survive and reproduce. Less is known about the shape of TPCs for traits that are not linked to aerobic metabolism, although they may also show a bell-shape due to effects of temperature on reaction kinetics and enzyme activity (Wilson et al. 2002; Norin et al. 2014).

While many studies have examined TPCs, there are some questions that are still not well resolved. Two common assumptions of TPCs are that thermal performance does not change across a species' range (i.e. no local adaptation) and that prior experience to thermal environments does not result in plasticity (Sinclair et al. 2016). This means that many studies have only focused on only one population, instead of comparing across populations, and that organisms are reared under one set of thermal conditions, instead of examining how rearing temperature can influence performance. While scientists may not believe these assumptions to be true, many experimental designs fail to account for these

differences. A common problem in these thermal ecology studies is when conclusions are draw for an entire species, without accounting for these differences that can arise across populations or when organisms face varying thermal environments.

TPCs can be a useful tool for biologists to gain a better understanding of how organisms will respond across a range of temperatures (Huey and Stevenson 1979). Due to the threat of climate change, there has been renewed interest in TPCs because they can be used to predict success of species and populations under different temperature scenarios (Huey and Kingsolver 2011; Schulte et al. 2011; Muñoz et al. 2015). Understanding the relationship between ectotherms and raising temperatures will only become more important as organisms are pushed closer to their upper critical temperatures.

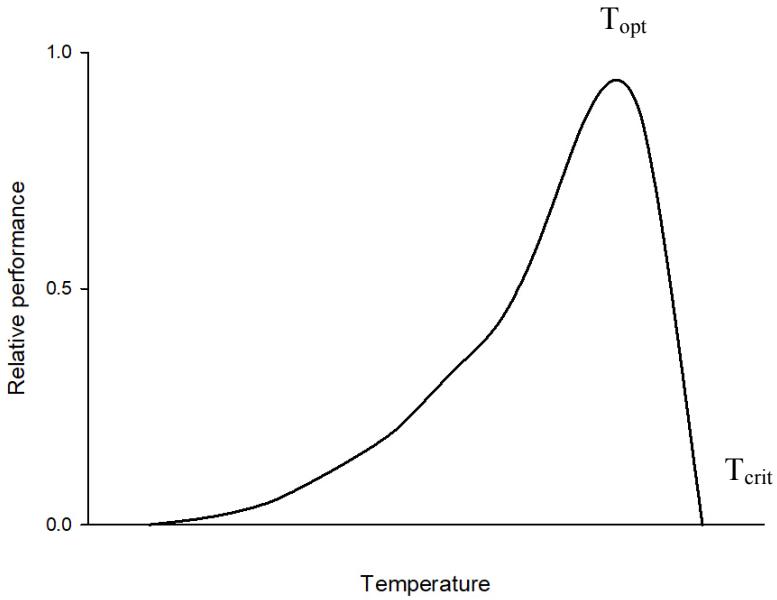

Figure 1: A hypothetical thermal performance curve showing optimal temperature (T_{opt}) and upper critical temperature (T_{crit}), adapted from Huey & Stevenson (1979).

1.4 Locomotion

Temperature influences locomotion in lizards (Huey 1982; Xiang et al. 1996; Zamora-Camacho et al. 2015), amphibians (Arendt 2003; Arendt and Hoang 2005), and fish (Brett 1964; Beamish 1966; Batty and Blaxter 1992), with lower and upper temperatures constraining movement. Two ways movement can be fueled is through either glycolytic or oxidative pathways. Glycolytic metabolism fuels anaerobic movements such as quick bursts used in predator avoidance or prey capture (Domenici and Blake 1997). Oxygen is not required to generate the energy needed to fuel these movements (Hargreaves 1995). Oxidative metabolism fuels aerobic movements that need to be sustained for longer periods of time, such as long distance running or swimming (Farrell et al. 2009). Oxygen is required to generate the energy to maintain these movements (Hargreaves 1995).

The two main types of skeletal muscle fibers in fish are fast-twitch and slow-twitch (Johnston 1999). Fast-twitch fibers are associated with glycolytic metabolic pathways. These fibers are associated with high-speed swimming for short periods of time. Slow-twitch fibers are associated with oxidative metabolic pathways (Johnston 1999). These fibers are associated with routine swimming, such as for foraging and migration. Embryonic fish have proportionately more slow-twitch muscle fibers compared with older fish that have more fast-twitch fibers (Vieira and Johnston 1992). Therefore, proportional amounts of each type of muscle fiber can change as fish grow and develop. Fish can increase muscle size as well as number of muscle fibers throughout their lives (Stickland 1983). Therefore, changes in water temperatures after fish are hatched can still affect muscle development.

The heart is important for aerobic performance because it is the organ that circulates oxygen-carrying blood around the body. In fish, oxygen is taken up from the water through the gills by the process of diffusion. Blood is transported around the body delivering this oxygen and when it reaches the heart, it is pumped back to the gills to uptake more oxygen. When temperature is increased, heart rate increases (Farrell et al. 2009). This increased demand on the heart can cause physiological changes to the heart over time.

Previous studies have shown that it is the heart's ability to pump oxygen to surrounding tissues that limits oxygen in the body, not oxygen uptake at the gills or tissue utilization (Penney et al. 2014). Over the period of a few months, temperature can affect relative ventricular mass (mass of the ventricle compared to the body mass), cardiac pacemaker rate (generates action potentials for the heart to contract), and thickness of the heart ventricle (Gamperl & Farrell 2004; Anttila et al. 2013; Anttila et al. 2015). Cardiac output is a product of heart rate (beats per minute) and stroke volume (amount of blood pumped) (Keen & Farrell 1994). Higher temperatures increase the oxygen demand of tissues. With a higher cardiac output, more blood is being circulated around the body, and more oxygen can be delivered at a faster rate to these tissues. In order to generate this increase cardiac output, changes in morphology will be observed. Therefore, differences in the heart may account for differences in aerobic performance observed.

1.5 Burst speed

Anaerobic locomotion is commonly measured by burst speed (Guderley and Blier, 1988). Burst speed is a quick movement that lasts for a short period of time (Guderley and Blier

1988). Burst speed has direct ecological relevance in predator avoidance and prey capture (Domenici and Blake 1997). Organisms that swim faster are more likely to avoid predator attacks. In *Pseudacris regilla* tadpoles, tadpoles that escaped attacks by predatory garter snakes (*Thamnophis sirtalis fitchii*) swam almost twice as fast as tadpoles that were eaten by the snakes (Watkins 1996). Populations of mosquitofish (*Gambusia affinis*) that originated from areas with high predation had 20% faster burst speeds than populations with low predation, showing that fast burst speeds are an adaptive trait that can be selected for (Langerhans et al. 2004). Therefore, fast burst speed may be an important trait for predator avoidance.

Burst speed may also be important for predators to successfully capture prey (Arnold et al. 1991). For example, juvenile salmon feed by stationing themselves in areas of fast flowing streams, and then dart out to retrieve floating prey. Once food is captured, they are pushed downstream and must swim back to their original location to wait for their next prey item. Huey et al. (1984) found that species of lizards that used a sit-and-wait tactic for hunting had higher burst speeds than species that continuously actively foraged. Therefore, foraging style may also determine what species have faster or slower burst speeds.

For animals that move in water, two ways burst speed can be measured is through maximal velocity or a c-start (sometimes s-start), and authors will often refer to both of these movements as burst speed. Maximal velocity is the fastest velocity an organism can maintain over a short distance, whereas, a c-start is characterized by the curve of the body into a c shape at the beginning of a quick movement (s-start is the curve of the body in an s shape) (Dominici and Blake, 1997). Dominici and Blake (1997) state that all maximal

velocities begin with a c-start, but a fish could perform a c-start and not have a maximal velocity if they do not move. If movement forward does not follow the initial muscle contraction, then neither prey will be captured nor predators avoided. For my thesis I chose to measure maximal velocity, and will be referring to maximal velocity as burst speed for the rest of my thesis.

Early studies found burst speed to be independent of water temperatures; however, new studies are showing that the burst speed of certain species respond to water temperatures (Guderley and Blier 1988). Brett (1971) found burst speed to be independent of water temperatures in sockeye salmon (*Oncorhynchus nerka*), and Blaxter and Dickens (1959) found no consistent effect of water temperature on burst speed in herring (*Clupea harengus*). Whereas Rulifson (1977) found that water temperature followed a linear regression for burst speed for juvenile striped mullet (*Mugil cephalus*), spot (*Leiostomu xanthunrs*), and pinfish (*Lagodon rhomboids*). In contrast, Johnson and Bennett (1995) found that both goldfish (*Carassius auratus*) and killifish (*Fundulus heteroclitus*) had burst speeds that peaked at intermediate temperatures, with slower burst speeds at lower and higher temperatures, following a shape more consistent with aerobic activity. While researchers have assumed that burst speed is independent of water temperature because it is anaerobic, there appears to be some species-specific results.

Rearing temperature can cause changes in burst speed. Rearing temperature is the temperature that organisms face during their time of growth and development. For this thesis, rearing temperature is temperature applied to an organism in the juvenile stage over several months. Acclimation temperature is a temperature that the organism is subjected to over a short period. For this thesis, acclimation temperatures represent

temperatures applied from weeks to a couple of months in any life stage. For fish and amphibians mentioned in this thesis, this represents a relatively short period in the organism's entire life span. Arendt and Hoang (2005) found that *Spea hammondii* tadpoles reared at a cooler temperature had faster burst speed than those reared at a warmer temperature. Barramundi (*Lates calcarifer*) reared at the coolest water temperature outperformed individuals that were reared at warmer temperatures when tested at a cool water temperature (Norin et al. 2014). This relationship was not observed when these cold-reared individuals were tested at higher water temperatures, as individuals from all rearing temperatures performed equally as well. Claireaux et al. (2007) found that an increase of acclimation temperature from 12°C to 22°C resulted in a 21% mean increase in sprint speed of European sea bass (*Dicentrarchus labrax*) when tested at a common temperature of 15°C. Threespine sticklebacks (*Gasterosteus aculeatus*) were reared in either 8°C or 23°C water and tested at water temperatures of 8°C or 23°C in the spring and fall (Guderley et al. 2001). Differences in burst speed were only found at the 23°C water temperature. In the spring, the fish reared at the cooler temperature were faster, whereas in the fall, fish reared at the warmer temperature were faster. None of these studies looked at multiple temperatures across a wide range of water temperatures. Burst speed does demonstrate plasticity based on rearing temperature, but the direction and magnitude of effects appear to be species-specific.

Genetic adaptation may also lead to differences in burst speed based on differences in local environments. O'Steen et al. (2002) found that populations of guppy (*Poecilia reticulata*) from high predation streams had higher survival than populations from low predation streams in the presence of a natural predator. Survival was linked to

escape ability, which would include burst speed as well as evasiveness. As described above, mosquitofish populations that frequently encountered high predation had faster burst speeds than mosquitofish populations that came from areas with low predation (Langerhans et al. 2004). Populations from high predation areas had larger caudal regions, smaller heads, and more elongated bodies, which would improve the hydrodynamics of these fish and could contribute to the increased burst speed. Therefore, differences in predation risk have led to differences in body morphology that can affect burst speeds.

1.6 Critical swim speed

Prolonged swimming is commonly measured by critical swim speed (a test developed by Brett (1964), where water velocity is incrementally increased until the fish reaches exhaustion), and represents prolonged swimming. Prolonged swimming is important for fish during routine swimming and long migrations (Guderley & Blier 1988). In juvenile salmon, prolonged swimming is important for moving around the stream and finding suitable areas to station themselves for feeding (Leavy & Bonner 2009). At temperatures approaching their upper thermal limits, fish will be unable to sustain aerobic swimming (Brett 1967). In salmonids, prolonged swimming is most important during upstream migrations to spawning grounds. Warm river temperatures have been linked to failed upstream migration (Farrell et al. 2008), which prevent reproduction from occurring.

Critical swim speed requires the use of oxygen to sustain this prolonged swimming. Critical swim speed is also associated with the heart's ability to supply oxygen to tissues to maintain swim performance (Franklin et al. 2007). Atlantic salmon

with greater thermal tolerances have been found to have higher hematocrit (percentage of red blood cells relative to total blood volume) (Gradil 2015), larger heart ventricles (Anttila et al. 2013; Anttila et al. 2015), and more myoglobin (oxygen-binding protein in muscle) (Anttila et al. 2013), which may all aid in supplying more oxygen to the body.

The oxygen and capacity limited thermal tolerance (OCLTT) hypothesis states that aerobic performance is limited by oxygen, and is the basis for a growing field of work that examines the heart as it relates to aerobic performance (Pörtner 2001, Pörtner & Farrell 2008, Pörtner 2010). Previous studies on salmon have used heart rate as a proxy for aerobic performance, which can be used to rapidly assess optimal temperature and upper critical temperature (Casselman et al. 2012). Multiple studies have found aerobic performance results consistent with the OCLTT framework (Farrell 2009, Anttila et al. 2014, Gradil et al. 2015). However, there have been many criticisms of the OCLTT. Juvenile barramundi, pink salmon (*Oncorhynchus gorbuscha)*, and Atlantic halibut (*Hippoglossus hippoglossus*) maintain aerobic scope at temperatures above those ecologically relevant, but other aerobically driven activities such as growth or reproduction are unable to occur at these high temperatures (Clark et al. 2011, Gräns et al. 2014, Norin et al. 2014). This mismatch between aerobic scope and other aerobic activities shows that oxygen delivery is not the limiting factor, as would be predicted by the OCLTT.

Critical swim speed has been shown to peak at intermediate water temperatures, and decrease at upper or lower water temperatures, which follows the classic shape of a TPC. This relationship was highlighted by Brett (1967) in sockeye salmon and in coho salmon by Griffiths and Alderdice (1972). The optimal temperature for sockeye salmon

was 15°C and for coho salmon ~20°C, with slower swim speeds at higher and lower water temperatures. In contrast, Wilson et al. (2002) examined the Antarctic fish *Pagothenia borchgrevinki* and found that critical swim speed peaked at the lowest water temperature (-1°C), and declined with temperatures approaching 8°C. Therefore, TPCs for critical swim speed typically follows a bell-shape curve, but this is not true for every species.

Critical swim speed has been shown to respond to rearing temperature. Striped bass (*Morone saxatilis*) were acclimated to 9°C or 25°C and performed critical swim speed tests at a common temperature of 15°C (Sisson and Sidell 1987). Bass acclimated to 9°C had a higher critical swim speed than bass acclimated to 25°C. The authors suggest this increase in critical swim speed is due to the cold acclimated fish delaying the need for fast-twitch muscle fibers that are used as after slow-twitch muscle fiber begins to fatigue. In coho salmon, acclimation temperature changed the shape of the TPC, and slightly changed the optimal temperature, but most fish still had an optimal temperature around 20°C regardless of acclimation temperature (Griffiths and Alderdice 1972). Sockeye salmon had an optimal temperature of 15°C when acclimated to 15°C (Brett 1967). Sockeye salmon acclimated to temperatures of 5°C to 25°C and tested at their acclimation temperature still had the fastest critical swim speed at 15°C, but the shape of the TPCs changed. Fish acclimated to 5°C swam faster than fish acclimated to 15°C when tested at 5°C. Fish acclimated to 25°C swam faster than fish acclimated to 15°C when tested at 25°C. This relationship was not observed at intermediate acclimation and test temperatures of 10°C and 20°C. Rearing temperature can change the maximum

critical swim speed for an organism, as well as the performance across a range of temperatures.

1.7 Temperature Preference

Ectotherms rely on the environment to control their body temperatures, however, they are also constrained to certain environments based on food availability, predation, mating opportunities, or physical barriers. There are many hypotheses as to what determines an organism's preferred temperature, and I will briefly describe three of them: the coadaptation, suboptimal is optimal, and trait variation hypothesis. The coadaptation hypothesis states that an organism should prefer a body temperature that maximizes Darwinian fitness by choosing a temperature close to the organism's optimal temperature (Angilletta et al. 2002). Haupt et al. (2017) found that *Pringleophaga marioni* caterpillars preferred a temperature that aligned with survival and optimal feeding, but not movement. A study conducted on roach (*Rutilus rutilus*) also found preferred temperature to coincide with optimal temperature for feeding, growth, and energy conversion (Van Dijk et al 2002). In a study on Australian skinks, preferred temperature only partially matched optimal temperature for sprint speed (partial coadaptation for sprint speed) (Huey and Bennett, 1987). The suboptimal is optimal hypothesis states that ectotherms should prefer temperatures below their optimal temperature, as ectotherms are not good regulators, and organisms must buffer against reaching the upper critical temperature (Martin and Huey 2008). This work has support from multiple species of beetle and flies, where the preferred temperature is lower than the optimal temperature for population growth (Martin and Huey 2008). Another hypothesis is that organisms may prefer temperatures that will relate to overall survival, which means preferred temperature will

depend on the trait that is most limited-this is called the trait variation hypothesis (Huey and Stevenson, 1979). Killen (2014) found the common minnow (*Phoxinus phoxinus*) supported this hypothesis, as feeding history altered the preferred temperature of these fish based on what was most necessary. Fish that were food deprived preferred a lower temperature than fish fed daily to satiation. This was hypothesized to divert energy away from SMR to allow for compensatory growth, as metabolism lowers with lowered temperature. All of these hypotheses examine how performance relates to temperature preference, but when looking at multiple performance measures, they may not all align with temperature preference.

Vertical or horizontal gradients have been used to measure temperature preference in invertebrates (Neill et al. 1972). These gradients allowed the organisms to move around and then settle at a temperature that would be deemed their preferred temperature. However, the effectiveness of these methods for highly mobile fish has been questioned, as it is uncommon for active fish to naturally stop moving in their habitats (McCauley, 1977). Neill et al. (1972) invented the first shuttlebox, which was an alternative way to measure temperature preference in fish. This shuttlebox had two chambers with a tunnel between them whose opening was lined with photocells. When the beam of photocells was broken, the system would register the fish had moved sides. There is a 2°C difference between the chambers, with one side being warmer than the other. When the fish passed to the warmer side, the whole system would warm, at 3-5°C per hour, and when the fish passed to the cooler side, the whole system would cool at that same rate. Neill et al. (1972) used this system on 6 species of freshwater fish. Further studies would

then continue to use this same system for fish research (Schurmann and Steffenson 1992, Konecki et al. 1995, Killen 2014, Nay et al. 2015).

Rearing environment can affect temperature preference in many different ways. O'Steen (1998) found that snapping turtles (*Chelydra serpentine*) preferred temperatures opposite to the temperature they were incubated at (warm incubated turtles preferred cooler water temperatures, while cold incubated turtles preferred warmer water temperatures). In another study, coral reef cardinalfish (*Cheilodipterus quinquelineatus*) were acclimated to two different temperatures and there was no difference found in their preferred temperature (Nay et al., 2015). However, both groups preferred a temperature that matched their average summer temperature in the wild. Javaid and Anderson (1967) examined juvenile Atlantic salmon and rainbow trout and found that their preferred temperature was slightly higher than their acclimation temperature. Organisms can respond to different rearing environments by sometimes altering their temperature preference, but sometimes it has no effect at all.

Temperature preference may also vary across populations. Killifish from northern populations had higher preferred temperatures than southern populations (Fangue et al. 2009). Conversely, in *Drosophila immigrans* lines there was no difference in temperature preference across populations (Yamamoto 1994). While in some species, populations differ in their temperature preference, in other species temperature preference does not differ, so one cannot extrapolate the temperature preference of populations of a species that has not previously been studied.

1.8 Atlantic salmon

Atlantic salmon are a top predator in the aquatic ecosystems in which they reside and once supported a valuable fishery throughout their native range (Parrish et al., 1998). Atlantic salmon spawn in streams, where the juveniles remain for their first one to seven years before migrating out to deeper water (Keenleyside and Yamamoto 1962). Atlantic salmon may be either potamodromous or anadromous (Dimond and Smitka 2005). Potamodromous salmon stay in fresh water their entire lives, migrating from streams to lakes, while anadromous salmon migrate out to the ocean. Before migrating, salmon undergo the process of smoltification, where they change color and develop the ability to osmoregulate (Keenleyside and Yamamoto 1962). Atlantic salmon will then swim downstream out into the lake or ocean until they are ready to spawn. When they are ready to spawn, salmon will swim upstream to return to their native stream to lay eggs. Atlantic salmon are repeat spawners and display natal site fidelity (Jonsson et al 2001).

Stream life is an important part of the life cycle for an Atlantic salmon because they are subject to high predation and variable water temperatures. Atlantic salmon are territorial visual feeders (Arnold et al. 1991, Migaud et al. 2007). They hold onto rocks using their pectoral fins and feed on drifting invertebrates. This exposes them to predators, so their cryptic colouration and ability to hide allows them to survive (Arnold et al. 1991, Walker et al. 2005). Predation is high during the in-stream part of Atlantic salmon life, as most predators are gape-limited and salmon are small enough during this life stage to be eaten (Armstrong et al. 2013). Water temperature can also play a role in survival, as water temperatures too high or too low can affect embryonic development, juvenile growth, and ability to feed (Armstrong et al. 2013).

In Atlantic salmon, acclimation temperature can affect thermal tolerance and aerobic thermal performance. The thermal tolerance range (range of temperatures an organism can survive at) is 0-33°C (Elliott 1991). Atlantic salmon cope with near freezing water temperatures in the winter, especially in the egg stage. However, many Atlantic salmon will not survive at water temperatures of 33°C unless they have been acclimated to warmer temperatures over time, or are only exposed for a very short period of time. The upper incipient lethal temperature (the temperature an organism can be at for a considerable length of time, in this study 7 days was used) of Atlantic salmon was found to be 27.8°C when acclimated to a temperature of 27°C (Elliott 1991). Fish acclimated to 5°C had an upper incipient lethal temperature only 4°C cooler, showing that there is plasticity in thermal tolerance, but there is a limit to upper temperatures that these fish can tolerate. Fish acclimated to 20°C fed normally between 7-22.5°C, but fish acclimated to higher temperatures of 25°C and 27°C did not feed at all. While fish may be able to survive at high temperatures (upwards of 25°C), if they cannot feed at these temperatures, then they will not survive for long in the wild. It is important that salmon maintain their ability to swim, so that they escape areas when temperatures are unfavourable. Temperature has a large pronounced effect on survival and aerobic capacity in Atlantic salmon.

Aerobic performance of Atlantic salmon is also constrained by temperature. Anttila et al. (2014) used heart rate as a proxy for aerobic performance to determine optimal temperature and upper critical temperature of Atlantic salmon. They found plasticity in both proxies for optimal temperature and upper critical temperature when fish were acclimated at an 8°C difference. The highest upper critical temperature was

27.5°C, which is similar to the upper incipient lethal temperature found by Elliot (1991), whereas the optimal temperature was between 16-19°C. Gradil et al. (2016) examined three populations of Atlantic salmon (including the LaHave and Sebago populations) and found that populations differed in a rank order of aerobic optimal temperatures that corresponded with average summer water temperatures. Upper critical temperatures ranged from 23.5-26.4°C, and the optimal temperatures ranged from 14.7-17.0°C. This study was the first to show local adaptation to temperature in Atlantic salmon. Therefore, the aerobic performance of Atlantic salmon is both constrained by temperature and can change across rearing environments or populations.

Temperature preference of Atlantic salmon has also been previously studied, and varies across populations. Javaid & Anderson (1967) found that acclimation temperature could affect preferred temperature of juvenile Atlantic salmon from the Miramichi population. Preferred temperatures aligned with acclimation temperatures. In another study, the preferred temperature of potadromous New Brunswick Atlantic salmon fry was 13.6°C and anadromous salmon was 13.8°C (Peterson et al. 1979). Both of these groups were acclimated to temperatures of ~12°C. Two populations of landlocked Atlantic salmon from Newfoundland moved out of areas where water temperature exceeded 14°C, suggesting their preferred temperature is below this value (Leggett and Power 1969). The preferred temperature of Atlantic salmon differs based on rearing conditions and across populations.

In Canada, Atlantic salmon are listed under the Species at Risk Act ranging from threatened to extinct across the country (COSEWIC, 2006). In the Great Lakes, Atlantic

salmon were extirpated by 1896 (Parsons, 1973). Despite over 100 years of stocking effort into the Lake Ontario, no self-sustaining populations have been established. A current goal of the Ontario Ministry of Natural Resources and Forestry (OMNRF) is to establish self-sustaining populations, and thus, more research must be done to discover and mitigate the causes of the low success rate of the stocked populations (OMNRF 2015).

1.9 Experimental design

I examined burst speed and critical swim speed of juvenile Atlantic salmon reared at two temperatures across a range of water temperatures. I then use these data to examine the characteristics of the resulting TPCs. I measure these traits in two populations that are currently being used for stocking efforts in Lake Ontario. I also look at temperature preference of these two populations reared at two temperatures.

The first objective of this project was to determine how burst speed and critical swim speed would be affected by water temperature. For burst speed, I hypothesized that performance would be maintained across water temperatures because it is necessary for survival of juvenile salmon to avoid predators and capture prey. I predicted that burst speed will be unaffected by water temperatures, so it will not follow the classic bell shape of TPCs. For critical swim speed, I hypothesized performance would be maximized at an intermediate temperature, as aerobic scope and cardiac performance have been found to decline at higher temperatures as described by the OCLTT (Brett 1964, Anttila et al. 2013, Muñoz 2014). I predicted that Atlantic salmon performance will follow the bell-shaped curve with an optimal temperature at an intermediate water temperature.

My second objective was to examine if Atlantic salmon display developmental plasticity in burst speed, critical swim speed and temperature preference. I examined burst speed and critical swim speed of fish reared at two temperatures to determine if either trait showed plasticity. Plasticity could be shown in a difference in overall speeds of swimming between the two groups or through a shift in T_{opt} of the TPCs. For temperature preference, I hypothesized that Atlantic salmon would prefer temperatures that aligned with their rearing temperature, as was observed by Javaid & Anderson (1967) in the Miramichi Atlantic salmon population. I predicted that fish reared at cooler temperatures would prefer cooler temperatures, and the fish reared at warmer temperatures would prefer warmer temperatures. I did not have a prediction as to how the two populations would differ in performance, but I wanted to test if the results were consistent across two independent populations.

My third objective was to determine how optimal temperatures of burst speed and critical swim speed would relate to temperature preference. I wanted to determine if temperature preference would align with the coadaptation hypothesis, suboptimal is optimal hypothesis, trait variation hypothesis or support none of these hypotheses for burst speed and critical swim speed.

Methods

2.1 Experimental fish

Atlantic salmon from the Sebago Lake and LaHave River populations were examined in this study as they are two populations currently being stocked into Lake Ontario. The Sebago population is from Maine (43.9°N, 70.6°W) and is potamodromous (Dimond &

Smitka 2005). The LaHave population is from Nova Scotia (44.4°N, 64.5°W) and is anadromous (Dimond & Smitka 2005). These two populations have similiar water temperature regimes, with means at ~20°C and peaks at ~26°C throughout the summer (June-October) (Gradil, 2016). All fish were sourced from broodstock housed at the OMNRF Normandale Fish Culture Station (Vittoria, ON). The Sebago population has been held in Ontario Ministry of Natural Resources and Forestry (OMNRF) hatcheries for 3 generations, and the LaHave population for 6 generations (OMNRF, unpubl. data).

All experimental fish were produced at Normandale Fish Culture Station from November 2, 2016 to November 17, 2016. For each population, approximately 500-1000 eggs were collected from each of 30 four-year-old females and milt was collected from 30 males (three or four years old). Gametes were combined using a 1 male × 1 female breeding design (30 families for each population). Eggs were disinfected using two-step disinfection before and after water hardening using Ovadine (Syndel, Nanaimo, BC) (Torgersen & Håstein 1995).

Eggs from each population were placed in individual Heath trays separated by family and exposed to running water from a nearby creek with a temperature of approximately 8°C. The dead eggs were removed twice a week to prevent the spread of *Saprolegnia* spp. After hatch, before yolk sacs were completely absorbed, fish were transferred to Codrington Fisheries Research Facility (Codrington, ON) where they were held at approximately 12°C. Once fish transitioned to exogenous feeding, they were fed *ad libitum* with organic fish pellets (EWOS Commercial Feeds, Bergen, Norway).

On March 31, 2017, 100 fish from each population were transferred to Western

University to begin temperature treatments. Previous work by Anttila et al. (2014) showed ~6°C difference in cardiac collapse of Atlantic salmon reared at temperatures that differed by 8°C, so an 8°C difference that falls within the natural temperature range experienced by Atlantic salmon was chosen for this study. Specifically, 50 fish from each population were assigned to 68-L population-specific tanks at 11°C and 19°C, and were held at these temperatures for at least 5 months before beginning experiments. These tanks were supplied by tap water that had been run through carbon filters and nitrate removing bacteria. Daily 10% water changes were conducted for this recirculating system. This water was used for all other trials. Fish were set to a 12-hour day and night light cycle.

2.2 Burst speed

Burst speed trials were conducted in five tanks, each measuring 61 × 40 × 42 cm, with a water depth of ~4 cm. All tanks were part of a single recirculating system, with a VWR chiller (VWR, Illinois, U.S.A.) used to control water temperatures. Water was brought in from the hatchery. A 25% water change was conducted daily, and all tanks were cleaned before new fish were transferred into the burst speed tanks for the next block of trials.

Burst speed trials were conducted in blocks of five fish, with one fish per tank. Each block included one fish from each population at each rearing temperature, and one additional fish from a random treatment. To begin the block of trials, all burst speed tanks were lowered from room temperature (~17°C) to ~11°C. Fish from the 11°C rearing treatment were then transferred from the hatchery to the procedure room and placed into individual tanks. Water temperature was then increased at 1°C every 15 minutes until it

returned to 17°C. Fish from the 19°C rearing treatment were then placed individually into tanks. Fish were not fed on transfer days and were given 24 hours to recover in their burst speed tanks before beginning trials. Fish were fed on trial days after a minimum of three hours had elapsed since the end of trials.

Trials were conducted between 9:00-14:00 EST from September 22 2017 to March 3, 2018. To begin a trial, the water temperature was changed by 1°C every 15 minutes until the desired water temperature was reached. Trials were conducted at temperatures between 11°C and 25°C at 2°C increments. The order of water temperatures was randomized for each block (Appendix A). The water temperature in each tank was measured by an HH508 thermocouple (Omega, U.S.A.), and once all the water temperatures were within 1°C of the water temperature, trials would begin. During each burst speed trial the tanks were recorded from above using a camcorder that was placed on a shelf above each tank that had a hole for the lens to fit through (DCR-TRV150 HandyCam, SONY, New Jersey, U.S.A.). A motivator constructed from a 9V transistor was used to prod the tail of each fish and deliver a mild electric stimulus (Taylor & McPhail 1985). Fish were prodded up to five times to incite a burst, and if no burst was observed, the trial was deemed unsuccessful and excluded from further analysis. Each fish was motivated to perform a burst a total of three times at each water temperature, with a minimum of two minutes between bursts. After daily trials were completed, water temperature was returned to 17°C (room temperature) by changing 1°C every 15 minutes. In total, burst speed trials were conducted for 35 fish from the 11°C rearing treatment and 38 fish from the 19°C rearing treatment (Table 1).

At the end of each eight-day block, fish were removed from the burst speed tanks

and anesthetized using 1:1 ratio of MS-222 buffered with sodium bicarbonate. I then weighed and measured total length (snout to tip of caudal fin) of all fish. Sebago fish were tagged using visible implant elastomer tags (VIE; Northwest Marine Technologies, Shaw Island, WA) on either side of their dorsal fin for future identification during critical swim speed trials. Different colors and numbers of marks were used to create unique identification for each fish.

The start of a burst was identified by the presence of a C-start (Johnson & Bennett, 1995). Bursts where fish continually swam in a circle were excluded, as the maximum speed of the fish would not be accurately represented when turning. For frames 3-8, fish position was determined as the x and y coordinates of the snout of the fish using ImageJ version 1.51 (Schneider et al. 2012). Velocity in cm/s was calculated using Pythagorean theorem based on the position of the fish and time elapsed.

Due to a lack of consensus in the literature about how to calculate burst speed, I calculated burst speed using four different methods. For all methods I omitted the first frame as it was the starting position of the fish and no velocity could be calculated and the second frame because it often included the C-start movement, where the head of the fish would move, but the fish did not advance forward. The first method was to calculate burst speed as the maximum velocity observed during the first five frames. The second method was to calculate burst speed as the mean velocity of the first five frames. The third method was to calculate burst speed as the maximum velocity observed during the burst where the fish moved in a straight line. The fourth method was to calculate burst speed as the mean velocity across all frames during the burst where the fish moved in a straight line. Burst speed was calculated separately for each of the three bursts at a water

temperature and those values were then averaged prior to statistical analysis. These different analyses were used to examine differences between maximum and average speed, and determine how the start and end of a burst would affect burst speed.

2.3 Critical swim speed

Aerobic swim performance was assessed for only the Sebago population (due to time constraints) using a Loligo swim flume (Loligo Systems, Denmark, https://www.loligosystems.com). A motor connected to a spinning impeller generates a water current in a circular fashion around the flume (Appendix B). Water was brought in daily from the hatchery to fill the swim flume and holding tanks. The water passes through a diffuser to ensure laminar flow into the chamber where the fish is held. The swim chamber measured 40 × 10 × 10 cm. A mild electric stimulus could be applied to a metal grid at the back on the swim chamber to motivate fish when necessary. The swim flume was connected to a VWR chiller and a 68-L holding tank (with an aerator) half filled with water. Groups of fish were acclimated together and run through the same order of water temperatures (Appendix C). There was an overall sample size of 16 - ten fish from burst speed trials and an additional six fish. The order of metrics is described in the appendix (Appendix D).

There is a linear relationship between frequency (Hz) of the swim flume motor and velocity (m/s). Calibration curves were created using a flow meter (Höntzsch, Waiblingen, Germany) before each group was started, and these curves were used to calculate critical swim speed. Test fish were anesthetized using MS-222 (as described in the burst speed section) and a UV light was used to check elastomer tags to identify

individuals. Fish were moved to the burst speed tanks (one fish per tank) as housing during swim flume trials. Fish from the burst speed tanks were netted daily and transferred to the room where the swim flume was set up. I then transferred fish into individual holding containers within the 17°C housing tank. Water temperature was achieved by changing the water temperature at a rate of 1°C every 15 minutes. Swim trials were performed at the same temperatures as burst speed (11°C and 25°C at 2°C increments) in a semi-randomized order. Four fish from the first group (all reared at 11°C) died after being exposed to 25°C test temperatures in the swim flume. Thus, for future groups of fish, 23°C was the highest water temperature used for fish reared at 11°C. The fish reared at 19°C were tested at 23°C and 25°C for the last two days of trials within a group. All other water temperatures were randomized.

Once the swim flume water reached the water temperature for that day, fish were netted and transferred to the swim flume chamber and allowed to swim at 0.12 m/s for three minutes to acclimatize to the system. At 2-minute intervals the water velocity was increased by 0.06 m/s. When a fish stopped swimming and was forced against the back of the chamber, it received a mild electric stimulus for 1 s. If a fish was stimulated twice in a row without moving (3 s between stimuli), then the fish was deemed exhausted and the trial was concluded for that day. The flow was then set to 0.12 m/s and the fish was allowed to recover for 3 min before returning it to the holding tank. After all fish completed their swim trials, the holding tank temperature was brought back to 17°C at 1°C per 15 minutes. Fish were then returned to their individual housing tanks. Fish were fed only after a minimum of 2 hours had passed since they were returned to their individual tanks.

Critical swimming speed (*Ucrit*) was calculated using the equation described by Brett (1964): $Ucrit = Ui + (Ti / Tii * Uii)$, where *Ui* is the highest velocity maintained for a full 2 min interval, *Ti* is the time of fatigue at last current velocity (min), *Tii* is the interval length (2 min), and *Uii* is the velocity increment (~0.06 m/s).

2.4 Temperature Preference

A shuttlebox was used to measured temperature preference (Neill et al. 1972). The shuttlebox was comprised of two white plastic chambers that were connected with an opening so a fish could swim between the chambers (Appendix E). The chambers were cylindrical with a diameter of 17 cm and 23 cm tall, with a water depth of approximately 4 cm. There was a 3°C difference between the two chambers: 9.5°C and 12.5°C for fish reared at 11°C; and 17.5°C and 20.5°C for fish reared at 19°C. After the habituation period, the system would ramp water temperature up or down at 0.3°C per minute. Using detection software and a camera, the position of the fish was recorded. At 1s intervals the temperatures of both chambers and the position of the fish were recorded. When the fish was in the cooler chamber, the entire system would cool maintaining the 3°C difference between chambers. When the fish was in the warmer chamber, the entire system would warm, again maintaining the 3°C difference between chambers.

After burst speed trials, one fish was placed into the shuttlebox, and the two chambers were kept at a constant temperature for one hour to allow for habituation. After one hour, the temperature in the two chambers would begin to change based on the position of the fish. Trials lasted 8 hrs. I calculated the average temperature that the fish experienced as the mean of the temperature in the chamber occupied by the fish at each 1 s recording

interval during the last 6.5 hr interval. I omitted half an hour after acclimation because fish from each rearing temperature (11°C or 19°C) started at different temperatures. I also calculated number of shuttles between the chambers for each fish. In total, I ran 46 fish through temperature preference trials- 8 LaHave from the 11°C rearing treatment, 11 LaHave fish from the 19°C rearing treatment, 15 Sebago from the 11°C rearing treatment, and 12 Sebago from the 19°C rearing treatment (Table 1).

2.5 Statistical analysis

All analyses were performed in JMP 13.0.0 (SAS Institute, 2016). I used a two-way ANOVA to compare the lengths of fish between rearing temperatures and population that completed trials for each metric. To examine how my four analyses of burst speed compared, I ran pairwise Pearson's correlations for each of the 4 burst speed calculations. To examine if water temperature, rearing temperature and population had an effect on burst speed, I performed a linear mixed effects model with population, rearing temperature, population × rearing temperature, water temperature, length, and fishID (random effect) as factors. Inter-invidual variation was calculated by dividing the amount of variation explained by fishID by the total variation in the model. I then tested critical swim speed for a linear and quadratic effect of water temperature between the two rearing treatments. I also examined how rearing temperature affected critical swim speed. I performed a linear mixed effects model with rearing temperature, water temperature, water temperature^2, rearing temperature × water temperature, rearing temperature × water temperature^2, length and fishID (random effect) as factors. To examine how rearing temperature and population affected temperature preference, I performed a linear model with population, rearing temperature, population × rearing temperature, length and

number of shuttles as factors.

Results

3.1 Study fish

I compared the mean body size of fish from each treatment that performed each swim performance metric (Table 1). For burst speed, fish from the LaHave population were significantly longer than fish from the Sebago population ($F_{3,69} = 6.97$, $P = 0.01$). Fish reared at 19°C were significantly longer than fish reared at 11°C ($F_{3,69} = 48.13$, $P < 0.001$). The interaction between rearing temperature and population was not significant ($F_{3,69} = 2.20$, $P = 0.14$). For critical swim speed, fish reared at 19°C were significantly longer than fish reared at 11°C ($F_{1,14} = 5.35$, $P = 0.037$). Fish reared at 19°C were longer than fish reared at 11°C for temperature preference trials ($F_{3,42} = 18.58$, $P < 0.001$), but there were no significant differences between the Sebago and LaHave population in length ($F_{3,42} = 3.85$, $P = 0.056$). The interaction between rearing temperature and population was not significant ($F_{3,42} = 0.45$, $P = 0.51$).

Table 1: Mean total lengths (± SD) and sample size (n) of juvenile Atlantic salmon (*Salmo salar*) from two populations (LaHave (LAH) and Sebago (SEB)) for three metrics. Means within a metric with the same letters are not significantly different ($P < 0.05$) according to Tukey's test.

	Population	Rearing temperature (°C)	Sample size (n)	Length (cm) ± SD
Burst speed	LAH	11	18	10.3 ± 3.0 c
		19	20	15.0 ± 2.7 a
	SEB	11	17	9.6 ± 1.5 c
		19	18	12.7 ± 2.0 b
Critical swim speed	SEB	11	10	13.7 ± 1.3 b
		19	6	15.0 ± 0.8 a
Temperature preference	LAH	11	8	10.6 ± 3.1 bc
		19	11	14.1 ± 3.0 a
	SEB	11	15	9.7 ± 1.6 c
		19	12	12.2 ± 1.8 ab

3.2 Burst speed

The four methods I used to calculate burst speed resulted in values that were highly correlated (pairwise correlation coefficients r= 0.66 to 0.93). Consequently, I chose to focus on a single measure for all subsequent analyses (the maximum speed observed during the first five frames), which was the fastest speed that the fish swam during the initial phase of its burst.

Burst speed was significantly affected by length of the fish; as length of fish increased, burst speed increased ($F_{1, 68.51} = 48.12$, $P < 0.001$). Inter-individual variation accounted for 13% of the variance in the data. I found that there was no effect of water temperature on burst speed ($F_{1, 498.64} = 0.35$, $P = 0.55$) (Fig. 2). Rearing temperature did not affect burst speed ($F_{1, 68.52} = 0.03$, $P = 0.86$). Fish from the Sebago population were significantly faster than the LaHave population, having burst speeds that were on average 9% faster based on the model after controlling for body size ($F_{1, 68.73} = 4.92$, $P = 0.03$). There was no significant interaction between rearing temperature and population ($F_{1, 68.53} = 1.03$, $P = 0.31$).

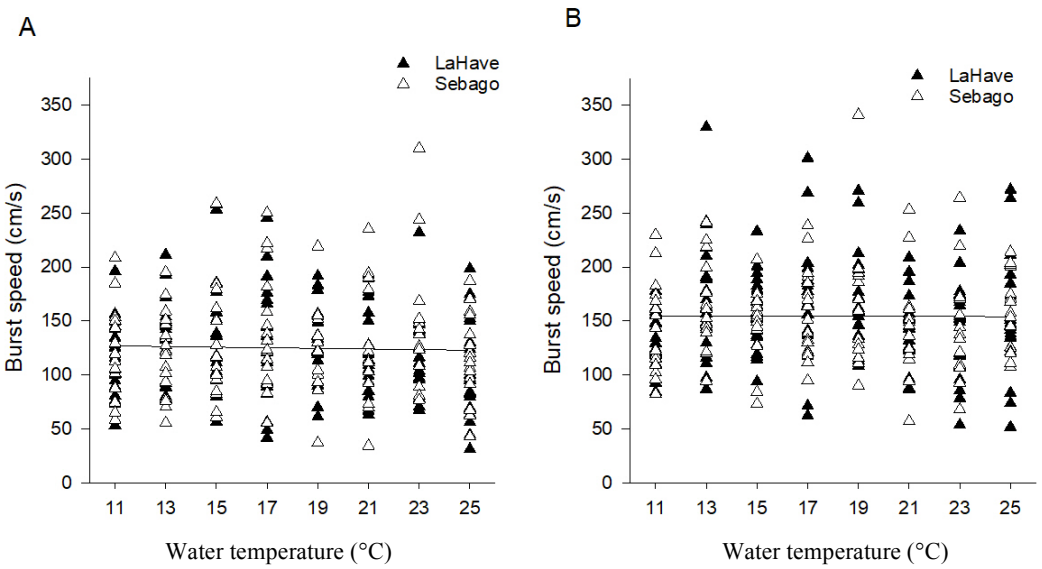

Figure 2: Burst speed (cm/s) as a function of water temperature for juvenile Atlantic salmon (*Salmo salar*) reared at (A) 11°C or (B) 19°C. Lines represent a linear regression plotted through all points in each panel that are both non-significant.

3.3 Critical swim speed

Body length did not significantly affect critical swim speed ($F_{1, 14.61} = 1.84$, $P = 0.20$). Inter-individual variation accounted for 39% of the variance in the critical swim speed data. Fish from the two rearing treatments responded differently to water temperatures, as they differed in the slope of their linear term ($F_{1, 87.57} = 5.44$, $P = 0.022$), and quadratic term ($F_{1, 87.65} = 5.46$, $P = 0.022$). Critical swim speed was positively associated with water temperatures for fish from both rearing treatments, but the critical swim speed of fish reared at 19°C increased exponentially with water temperatures, while the critical swim speed of fish reared at 11°C plateaued from 19°C onwards (Fig. 3). On average, fish reared at 11°C were significantly faster than fish reared at 19°C ($F_{1, 13.12} = 5.74$, $P = 0.031$).

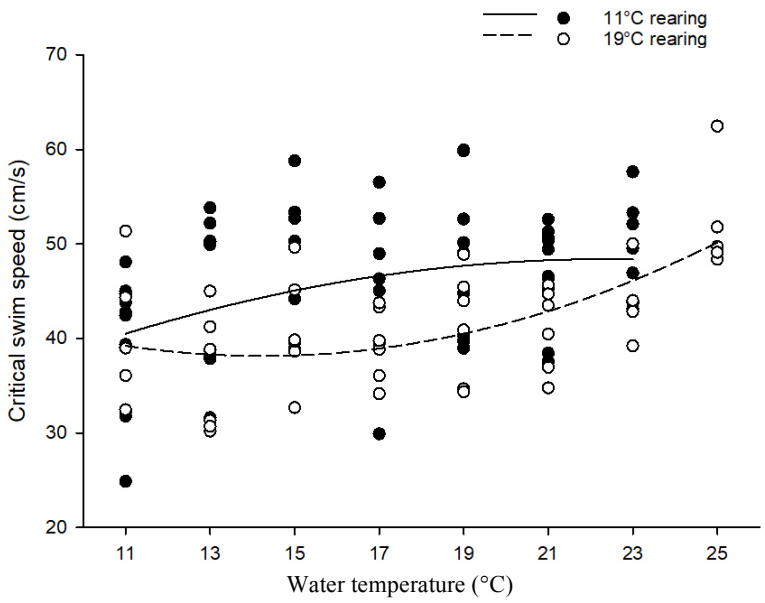

Figure 3: Critical swim speed (cm/s) as a function of water temperature for juvenile Atlantic salmon (*Salmo salar*) from the Sebago population. Lines represent quadratic regressions plotted through the points for each rearing temperature. The equation of the line for the fish reared at 11°C is $y = -0.061x^2 + 2.73x + 17.83$. The equation of the line for the fish reared at 19°C is $y = 0.104x^2 - 2.94x + 59.05$.

3.4 Temperature preference

An example of the raw data can be found in Appendix F. Length and number of shuttles did not affect mean experienced temperature ($F_{1,40} = 1.17$, $P = 0.29$; $F_{1,40} = 1.43$, $P = 0.24$). Fish reared at 19°C had a higher mean experienced temperature than fish reared at 11°C ($F_{1,40} = 9.97$, $P = 0.003$, Fig. 4). The Sebago population and LaHave population did not differ in their mean experienced temperature ($F_{1,40} = 0.0028$, $P = 0.96$). However, there was a significant interaction between population and rearing temperature with respect to mean experienced temperature ($F_{1,40} = 8.72$, $P = 0.005$). The Sebago fish reared at 19°C had significantly higher mean experienced temperatures than the Sebago fish reared at 11°C (17°C vs. 12°C), while the mean experienced temperature of the LaHave fish did not change based on rearing temperature (~14°C) (Fig. 4).

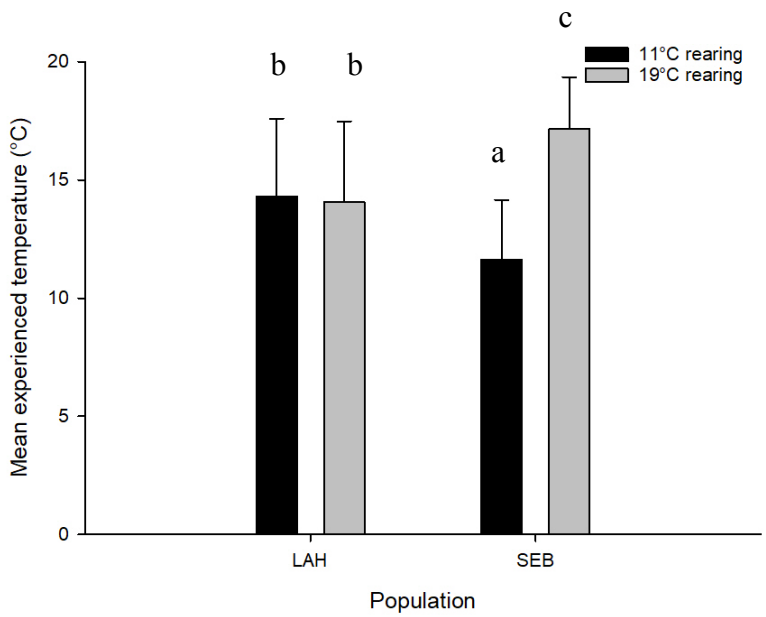

Figure 4: Comparison of mean experienced temperature (°C) of juvenile Atlantic salmon (*Salmo salar*) that conducted shuttlebox temperature preference trials. Means followed by the same letter are not significantly different ($P < 0.05$) according to Tukey's test.

Discussion

Understanding the effects of temperature on locomotion is important as fish face increasingly changing thermal environments. The ability to swim is essential for capturing prey, avoiding predators, and seeking out suitable microhabitats. While many studies have examined temperature and locomotion in fish, few studies have examined the swimming across a wide range of ecologically relevant temperatures, or the degree to which swimming can display plasticity. In my thesis, I used two populations of Atlantic salmon that are currently being stocked into Lake Ontario to explore these relationships of temperature with burst speed and critical swim speed. I hypothesized that burst speed would be maintained across water temperatures, and that critical swim speed would peak at intermediate temperatures. I examined plasticity in swim performance by looking across two rearing temperatures, and considered two populations that have different life histories. Lastly, I looked at temperature preference to see if optimal temperature of burst speed or critical swim speed followed the coadaptation hypothesis, suboptimal is optimal hypothesis or trait variation hypothesis.

4.1. Burst speed is independent of water temperature

In juvenile Atlantic salmon, I found no effect of water temperature on burst speed. Burst speed did not increase at warmer temperatures, and there was no indication that burst speed was higher at intermediate temperatures. In my results, I presented absolute burst speed (cm/s), but when looking at relative burst speed (BL/s), there is also no change in burst speed across water temperatures (Appendix G). My study thus provides no evidence that the relationship between burst speed and water temperature can be described by a

typical bell-shaped thermal performance curve, and I found support for my hypothesis that burst speed is maintained across the water temperatures tested. Studies in juvenile sockeye salmon (Brett 1964, Brett 1971) and adult herring (Blaxter and Dickson 1959) also found no effect of water temperature on burst speed. In contrast, burst speed of adult goldfish and killifish peaked at intermediate temperatures and followed a typical thermal performance curve shape (Johnson & Bennett 1995). In juvenile striped mullet, spot, and pinfish, burst speed increased linearly across water temperatures, but did not show a decline at high temperatures as expected for a typical thermal performance curve (Rulifson 1977). The effect of water temperatures on burst speed differs between species, and thus, the corresponding thermal performance curves take on different shapes across species.

Differences among studies in the sensitivity of burst speed to water temperature may be linked to differences in the foraging styles of the studied species. Atlantic salmon, sockeye salmon and herring all feed on fast-moving prey such as drifting invertebrates and other fishes (Wańkowski 1981; Checkley 1982). In contrast, goldfish, killifish, striped mullet, spot, and pinfish typically feed on slow-moving items such as detritus, benthic invertebrates, and zooplankton (Collin 1985; Godin 1986; Scholz 1991; Luczkovich et al. 1995; Mennigen et al. 2010). Capturing fast-moving prey requires a rapid burst towards the prey items (Rosenthal & Hempel 1970; Wańkowski 1981), whereas feeding on the slow-moving prey occurs by suction feeding or by digging through substrate (Luczkovich et al. 1995; Scholz 1991). Fishes that feed on fast-moving prey may thus be under strong selection to maintain near maximal burst speeds across the range of temperatures that they typically experience to maintain their ability to capture

prey, whereas fishes that feed on more stationary prey may be under weaker selection to maintain burst speeds at a full range of temperatures.

Alternatively, the difference in the sensitivity of burst speed to water temperature observed in these studies may be linked to differences in the structure of the environments in which these species live. Juvenile salmon live in fast-flowing streams and adult herring in pelagic zones of oceans, whereas the other fishes live in estuaries. Streams and oceans are associated with minimal vegetation and low turbidity (Bjornn & Reiser 1991; Crump et al. 1999; Mannino & Harvey 2000), whereas estuaries are associated with high turbidity and plentiful submerged vegetation (Blaber & Blaber 1980; Orth & Moore 1984). High turbidity and plentiful vegetation will provide more opportunities for prey to hide from predators (Abrahams & Kattenfeld 1997; Heck & Thoman 1981). This results in reduced need for the prey to use burst swimming to evade predators. Rapid burst speed across a full range of environmental temperatures may thus be under weaker selection in these estuarine fish relative to the marine or stream fish. Regardless of the specific mechanisms underlying differences in the relationship between water temperature and burst speed among species, my results provide support that Atlantic salmon are among the species for which water temperature does not have a significant effect on burst speed.

4.2. Burst speed does not exhibit plasticity based on rearing temperature

The rearing temperatures that individuals experience early in life are predicted to affect burst speed if this trait shows phenotypic plasticity. One way to exhibit this plasticity

would be a shift in the optimal temperature of burst speed across the range of temperatures tested. I did not observe this shift, likely because the relationship between water temperature and burst speed did not follow the shape of a thermal performance curve. My study is among the first to examine the effect of rearing temperature on burst speed across a wide range of temperatures. Independent of the expectation that optimal temperatures for burst speed would be affected by rearing temperature, I also found no main effect of rearing temperature on burst speed. These results contrast with previous studies of other ectotherms that showed plasticity in burst speed based on rearing temperature. In tadpoles, individuals reared at cooler temperatures had faster burst speeds than those reared at warmer temperatures (Arendt & Hoang 2005). Barrramundi reared at cooler temperatures swam faster than individuals reared at warmer temperatures when both groups were tested a low temperature, but there was no difference in burst speed when the groups were tested at warmer temperatures (Carey & Franklin 2009). In European sea bass, individuals reared at warmer temperatures had faster burst speeds than those reared at cooler temperatures (Claireaux et al. 2007). Guderley et al. (2001) found that threespine sticklebacks reared at warmer temperatures had faster burst speeds in the fall, while fish reared at cooler temperatures had faster bursts in the spring. None of the above-mentioned studies constructed thermal performance curves, either due to lack of water temperatures or because different hypotheses were being tested. Therefore, rearing temperature appears to have an increasing, decreasing and no effect on burst speed dependent across species. In Atlantic salmon, increased rearing temperature does not result in a shift in T_{opt} or a change in overall speed of burst speeds.

Rearing temperature may result in physiological changes to the organisms that cause differences in burst speed, such as increasing number of muscle fibers used for swimming or upregulating glycolytic enzyme activity that create ATP to power muscle contractions. Muscle fibers are used for swimming, so an increase in number of fibers can lead to increase in swimming ability (Johnston 1999). Rearing temperature has been shown to affect the number of muscle fibers. Warm-reared tadpoles were found to have more muscle fibers in their tails than cold-reared tadpoles (Arendt & Hoang 2005). In Atlantic salmon, embryos reared at a lower temperature been shown to have more fast-twitch muscle cells than their warmer counterparts (Stickland et al. 1988), yet my Atlantic salmon reared at colder temperatures did not swim faster than salmon reared at warmer temperatures. This may be because these muscle fibers were not fully developed. Arendt & Hoang (2005) found that warm-reared tadpoles had more muscle fibers, but they were undeveloped, so these warm-reared tadpoles were slower swimmers than the cold-reared tadpoles. Muscle enzyme levels have also been correlated with burst swimming, since these enzymes allow contractions to occur (Guderley et al. 2001). In threespine sticklebacks, rearing temperature resulted in differences in glycolytic enzyme activity (Guderley et al. 2001). However, Johnson & Wokoma (1986) found no effect of acclimation temperature on the glycolytic enzymes phosphofructokinase and lactate dehydrogenase in flounder, suggesting that glycolytic enzymes may respond differently to rearing temperature in different species. Based on my results, temperature does not appear to have a impact on burst swimming of Atlantic salmon, and based on the lack of difference in performance, I do not hypothesize that amount of muscle able to generate

swimming force or amount of glycolytic enzymes differ between my two rearing treatments.

4.3. Fish from the Sebago population have faster burst speeds than the LaHave population

Burst speed has been shown to differ across populations in various species of fish. Differences in burst speed among fish populations have been correlated to differences in amount of time in hatcheries or differences in body morphology (McDonald et al. 1998; Langerhans et al. 2004; Dayton et al. 2005). Fish raised in hatchery settings often perform worse than conspecifics from the wild. Wild-reared Atlantic salmon were found to have higher anaerobic capacity than hatchery-raised salmon, which would allow them to recover from anaerobic bursts quicker than hatchery reared salmon (McDonald et al. 1998). Hatchery-reared fish were found to have 40% less reproductive success than wild-reared fish (Araki et al. 2007), and smolts from wild stock survived twice as well as hatchery stock Atlantic salmon in the wild (Jonsson et al. 1991). In this study, the Sebago population had faster burst speeds than the LaHave population. The Sebago population has been reared in hatcheries for 3 generations, while the LaHave population has been reared in hatcheries for 6 generations. Therefore, the Sebago population may have faster burst speeds than the LaHave populations as they have been in the hatchery setting for less time, and this may be a trait that wild populations maintain more so than hatchery bred populations. Body morphology has been shown to affect burst speed as well. Mosquitofish populations that had high predation had a larger caudal region, smaller head, and more elongated shape that allowed them to have 20% faster burst speeds than conspecifics from low predator populations (Langerhans et al. 2004). Dayton et al. (2005)

found that larval tadpoles with a deeper tail fin and smaller body produced the fastest burst speeds compared with tadpoles of other body shapes. Elongation of the body appears to play a role in maintaining fast burst speeds. Body morphology was not examined in this study, but may have differed between populations, as the LaHave population was longer (see Table 1). Different amounts of time in a hatchery system and differences in body morphology may relate to differences in burst speed of Atlantic salmon.

4.4. Critical swim speed increases across water temperatures

In my study, the critical swim speed of juvenile Atlantic salmon consistently increased across the range of water temperatures that I tested. This relationship was observed when critical swim speed was presented in absolute (cm/s) (Fig. 3) and in relative (BL/s) (Appendix H) units. In contrast, studies of sockeye salmon (Brett 1967) and coho salmon (Griffiths & Alderdice 1972) found that critical swim speed was highest at an intermediate temperature, and was lower at both warmer and cooler temperatures. In the Antarctic fish *Pagothenia borchgrevinki,* the highest critical swim speed was observed at the lowest water temperatures, followed by a decrease in performance as temperatures increased (Wilson et al. 2002). In general, critical swim speed thus appears to be affected by water temperature, with the main difference among studies being whether or not a decline in critical swim speed at higher temperatures is observed.

Several factors may determine if a decline in critical swim speed is observed at high temperatures. Clark et al. (2013) has argued that the decrease in performance that

some researchers see in thermal performance curves for critical swim speed may be attributed to the onset of death. I did not observe a decline in performance for either of my rearing temperatures, however, some of my fish reared at 11°C died shortly after trials at the highest water temperature. There may be a narrow range of temperatures in which Atlantic salmon performance decreases. Juvenile Chinook salmon also demonstrated that up to 25°C aerobic scope remained consistent, even though fish began to die at these temperatures (Poletto et al. 2017). Munday et al. (2012) found that six species of cardinalfish maintained their high aerobic scope up to 32°C, despite being only 1°C away from their estimated lethal temperature. Atlantic salmon may demonstrate a similar response, where water temperatures need to be within 1°C of lethal temperatures to see a decrease in performance. Gradil et al. (2016) found the upper critical temperature (using a proxy of Arrhenius breakpoint temperature) of Sebago was 26.4°C. Based on these temperatures, the Sebago fish were more than 1°C away from their upper critical temperature when exposed to 25°C. A future study could test this hypothesis by performing critical swim speed trials up to 26°C at 1°C water temperature increments to see if a decrease in performance is observed.

Another factor that may affect the relationship between critical swim speed and water temperature is amount of time at each test temperature. I hypothesize I may have seen a decline in performance at upper water temperatures if my time at each speed was larger. My study used a modified critical swim speed protocol to decrease the amount of time to test each individual (0.06 m/s at 2 minute intervals). Conversely, Brett (1964) used 0.09 m/s velocity increases every 60 minutes, and Wilson et al. (2002) used 0.04

m/s every 10 minutes, which means my study had the shortest time intervals. However, a review of studies showed that previous critical swim trials have used time intervals ranging from 2-75 minutes, so my results fit within the protocols used in the literature (Hammer 1995). Length of each swim trial could also influence performance, as longer times at higher temperatures can stress the test subject and lead to decreased performance at lower temperatures. Kingsolver & Wood (2016) modeled the growth rates for the larvae tobacco hornworm (*Manduca sexta*) as a function of time at exposure temperature. The longer the exposure time to higher temperatures, the lower optimal and maximal temperatures for growth rates predicted. In these models, optimal temperatures decreased due to increased levels of heat shock proteins. A future study could examine how differences in amount of time at each water temperature can influence optimal and upper critical temperature of ectotherms, to determine a standard protocol, since this is an area of active research, and there appears to be no consistencies across researchers for durations of velocity increments (Hammer 1995). Therefore, water temperatures not close enough to upper critical temperatures and short duration at each water temperature may explain the lack of decreased performance observed at high water temperatures.

4.5. Complex relationship between rearing temperature and critical swim speed

Critical swim speed can also exhibit plasticity due to rearing temperature, which may influence maximum critical swim speed or the temperature at which critical swim speed is greatest. There is conflicting evidence as to how rearing temperature will affect critical swim speed. Sisson & Sidell (1987) found that striped bass acclimated to 9°C had a higher critical swim speed than fish acclimated to a 25°C temperature when tested at

15°C. This experiment did not construct a TPC as fish were only tested at the common temperature of 15°C. In juvenile coho salmon, fish acclimated to 2°C had critical swim speeds ~1 body length/sec slower than fish acclimated at 23°C at water temperatures of 17°C or 23°C, but these differences were not found when examining intermediate acclimation temperatures (8°C or 11°C) (Griffiths & Alderdice 1972). This study did not find a shift in optimal temperature, as all acclimation temperatures peaked at approximately 20°C, but fish acclimated to higher temperatures (20°C or 23°C) were able to swim at temperatures 3°C higher than fish acclimated to low temperatures (2°C or 5°C) before a decline in performance was observed. Brett (1967) also did not find a shift in the optimal temperature of sockeye salmon acclimated to different temperatures. Sockeye salmon acclimated to 5°C swam faster than fish acclimated to 15°C when tested at 5°C, but fish acclimated to higher temperatures outperformed the fish acclimated to 15°C at higher temperatures (Brett 1967). In my study, fish reared at 11°C swam faster than fish reared at 19°C overall. Therefore, increased rearing temperature does not appear to produce faster salmon, but it can allow these fish to maintain critical swim speeds at higher temperatures without a massive drop in performance. Rearing temperature does not appear to shift optimal temperature of critical swim speed.

Rearing fish at high temperatures can cause a decrease in performance due to negative effects on feeding. Atlantic salmon from Norway were acclimated at 3°C, 8°C, 13°C, 18°C or 23°C for four weeks and each acclimation group performed critical swim speed trials at their own temperatures (Hvas et al. 2017). Critical swim speed peaked at 18°C, and sharply declined for the 23°C group. However, fish acclimated to the 23°C

experienced high mortality compared to the other groups and also had trouble feeding during acclimation. This suggests this decline in performance of this group of fish may be due to poor condition of the fish before trials during the extended exposure to high temperatures. This poor condition was not observed in fish reared at 19°C in their study, and fish fed normally throughout their time before trials were conducted.

Rearing temperature may affect critical swim speed by affecting enzymes related to oxidative metabolism or amount of myoglobin. Succinic dehydrogenase (citric acid cycle and electron chain complex II), citrate synthase (citric acid cycle), and hexokinase (aerobic glucose utilization) are upregulated in slow-twitch muscle in cold acclimated fish (Sidell 1980; Johnson et al. 1985). When these cold acclimated fish are placed in warmer environments, they can display higher levels of enzyme activity than their warm acclimated counterparts.

Myoglobin binds and stores oxygen, which can then be released when needed by working muscles. Myoglobin was found to increase in cold acclimated goldfish, which can contribute to aerobic capacity, as it provides more available oxygen to the muscle cells while they are working (Sidell 1980). In European Atlantic salmon, cardiac myoglobin was significantly correlated with CT_{max} (critical thermal maxima), which is the temperature at which the organism loses equilibrium, and is related to T_{crit} (Anttila et al. 2013). Conversely, in Atlantic salmon from the Sebago and LaHave populations, myoglobin was not correlated with a proxy for T_{crit}, however, this study did have a small sample size (Gradil, 2015). Upregulation of aerobic enzymes and an increase in myoglobin may contribute to the increased critical swim speed observed in my Atlantic salmon.

4.6. Sebago fish display plasticity in temperature preference

Temperature preference may differ based on rearing temperature or across populations. In killifish, northern populations preferred warmer temperatures than southern populations (Fangue et al. 2009). In *Drosophila immigrans*, there was no difference in preferred temperature among populations (Yamamoto 1993). In Atlantic salmon from the Miramichi River in New Brunswick, salmon preferred temperatures that aligned with their acclimation temperature (Javaid & Anderson 1967). In my fish, the Sebago population preferred a higher temperature when reared at a higher temperature, while the preferred temperature of the LaHave population did not differ based on rearing temperature.

Plasticity in a variable environment is important because temperature preference has been linked to habitat choice (Fairbairn 1985, Krause et al. 1998). Higher variance in water temperature may correlate with a population having higher plasticity in temperature preference. Based on temperature data from Gradil et al. (2016) from the LaHave River and Sebago Lake, Sebago Lake has ~9% more variance in summer temperatures. This higher variation may partly explain why the Sebago population exhibits plasticity in temperature preference, while the LaHave population does not.

Differences due to their total generations in a hatchery may play a role in the difference in response to rearing temperature that I observed between populations. The LaHave population has been bred in hatcheries 3 generations longer than the Sebago population. The Miramichi population is caught as wild smolts and stocked out as adults, so multiple generations are never kept in a hatchery setting (Labadie 2016). Plasticity in

temperature preference of the LaHave population may have been lost through these generations in a hatchery because they are reared in a more thermally stable environment for a longer time. Without a thermally changing environment, there is no need to conserve this trait of plasticity in temperature preference. Changes in behaviour and physiology have been noted in other studies of fish comparing wild and hatchery raised fish, including differences in aggression, antipredator behaviours, brain size, and swimming ability (Huntingford 2004). Therefore, differences in variation of water temperatures of natal environments and amount of time in hatcheries may contribute to the differences in plasticity observed.

4.7. Temperature preference does not relate to optimal temperature of burst speed or critical swim speed

There are several hypotheses as to how optimal temperature of a trait may relate to temperature preference, such as the coadaptation hypothesis, suboptimal is optimal hypothesis, or the trait variation hypothesis. In my study, burst speed was unaffected by water temperature, so no optimal temperature was found. Critical swim speed linearly increased with temperature, so no clear optimal temperature was found for that trait either. Therefore, I was unable to find support for any of those hypotheses. The preferred temperature of Atlantic salmon may relate to traits other than locomotion. Jonsson et al. (2001) examined 5 populations of anadromous Atlantic salmon parr raised at 7-10°C. The optimal temperature for growth was determined to be between 16-20°C, the optimal temperature for maximum energy intake was 19-21°C, and the optimal temperatures for growth efficiency to be 12-18°C. Optimal temperatures for growth and maximum energy intake fit with the preferred temperatures of the Sebago fish reared at 19°C (preferred

temperature ~17°C), but not with Sebago fish reared at 11°C (~11°C) or either rearing temperature group of the LaHave fish (~14°C). The LaHave fish fit within the range for optimal growth efficiency, however, there was a large variance between the 5 populations studied (6°C) (Jonsson et al. 2001). Growth and metabolism may be related to temperature preference, which was found in sockeye salmon (Brett 1971). A future study could examine optimal temperatures for multiple traits to determine which one best aligns with preferred temperature in these populations of Atlantic salmon. Overall, optimal temperatures for swim performance were not found, so they do not relate to preferred temperature in Atlantic salmon.

4.8. Management Implications

Atlantic salmon reared at 11°C had a faster critical swimming speed compared to fish reared at 19°C. However, rearing Atlantic salmon at a cooler temperature may not benefit Atlantic salmon stocked into warmer streams, as it is important to consider how salmon will respond to temperatures near their upper critical temperature. Anttila et al. (2014) examined an 8°C acclimation difference, and found a 4.5-6.5°C difference in arrhythmic temperature (proxy for upper critical temperature). While upper critical temperature was not directly measured in this study, we can infer that the fish reared at 19°C had a higher upper critical temperature as none of them died after performing critical swim speed trials at 25°C, unlike the fish reared at 11°C. The Atlantic salmon in this study also differed in the way they responded to temperature for critical swim speed. The fish reared at 11°C initially linearly increased across temperatures and then plateaued, while the fish reared at 19°C continually increased exponentially, which resulted in the crossing of the two

regressions (fig. 2). Although, eventually the fish reared at 19°C would approach their upper critical temperature, and a decrease in performance would be observed at water temperatures past 25°C. Acclimation has also been found to affect the shape of thermal performance curves in sockeye and coho salmon (Brett 1967; Griffiths & Alderdice 1972). Therefore, rearing Atlantic salmon at a warmer temperature may benefit the fish when exposed to extreme heat events.

4.9 Significance of results

Thermal ecology is a large field that is gaining more attention as scientists try to understand patterns of biological diversity and predict how organisms will respond to climate change. My work examined TPCs of Atlantic salmon subjected to burst speed and critical swim speed tests. While is it commonly assumed that TPCs take on bell-shaped curves (Huey & Stevenson 1979), I found that this was not the case for burst speed or critical swim speed in Atlantic salmon. Instead, burst speed is independent of temperature, maintaining a maximal response across a wide range of temperatures, whereas critical swim speed continually increases with temperature, with fish reared at a higher temperature maintaining increase performance at upper temperatures. These results show the importance of examining the performance of species of interest, as many close-related species can behave differently during thermal performance experiments. It is also important to consider standardized protocols, as differences in methods can produce different results. I also found that the Sebago population displayed plasticity in temperature preference based on rearing temperature, while the LaHave population did not. This is an important finding for managers that stock these fish, as plasticity can be

beneficial for surviving in new habitats, such as a fish being stocked from a hatchery system into the wild.

4.10. Study limitations

The aim of this study was to determine how the performance of an individual fish would differ across water temperatures and different metrics (burst speed, critical swim speed and temperature preference). In order to obtain this data, a fish needed to be tested multiple times across multiple days. To minimize practice effects of burst speed and critical swim speed, water temperatures were randomized. However, I was only able to run five fish at a time through these randomized temperature sequences. This meant that to run all fish through these trials took several months, and during that time the fish had longer exposures to their rearing temperatures and continued to grow. Unfortunately, when running one individual through multiple metrics, there will always be the potential for impact on the results on the later metrics. Another limitation to this study is that fish completed burst speed trials before temperature preference, which may have impacted the results of temperature preference. Since temperature preference trials took an entire day to complete, fish within a block had different amounts of time between burst speed and temperature preference trials. This could only have been avoided if all fish could have been run at the same time (in five shuttle boxes), or if different individuals had been used across different metrics. In this study, I was unable to run the LaHave population in critical swim speed trials due to time limitations. If I could have repeated this experiment, I would be interested to compare the LaHave and Sebago population across critical swim speed.

4.11. Future Directions

My study focused on whole organism performance to gain a general understanding of how Atlantic salmon will respond to differences in water temperatures based on rearing temperature and population. However, this study did not examine underlying mechanisms that would explain differences in burst speed across rearing temperatures or populations or differences in critical swim speed based on rearing temperature. To test these mechanisms, a future study could rear salmon at two temperatures, and then measure the difference in glycolytic and oxidative muscle fiber contraction rates, functionality of fibers, glycolytic and oxidative enzymes, and then relate them to swim performance in salmon. This study could also then switch the temperature treatments between groups of fish to determine if this plasticity remains later in life, and the length of time needed to elicit this physiological change. This will give better insight into the mechanisms that cause the differences in swim performance observed.

Because my project was also tied to management goals of the stocking program of Atlantic salmon into Lake Ontario, further studies should examine if differences in swim performance increase survivorship of fish from one population or rearing temperature when stocked in streams. It is largely accepted that burst speed is linked to predator avoidance and prey capture in laboratory studies (Domenici & Blake 1997; Arnold et al. 1991), but it is less clear if faster burst speed will relate to overall increased survival in the wild. It is important to maintain critical swim speed over the range of temperatures a fish will experience in a wild, but again less clear if fish that can maintain high critical swim speeds over a large range of temperatures will result in increased survival and reproduction. A future study should relate swim performance in the lab to survival in the

wild to provide further evidence of how these laboratory studies translate into overall fitness in the wild.

4.12. Conclusions

I evaluated the hypotheses that burst speed and critical swim speed would be affected by rearing temperature, and that Atlantic salmon would prefer temperatures that corresponded to their rearing environment. While not associated directly with a hypothesis, I also examined fish from two populations. I found that burst speed was maintained across a wide range of water temperatures, while critical swim speed is influenced by water temperatures and the rearing temperature of the fish. I found that rearing fish at a colder temperature increases critical swim speed across water temperatures, but this increase starts to plateau at warmer temperatures. At these warmer temperatures, fish from the warmer rearing treatment still continue to increase their critical swim speed, so fish facing increasingly warming waters may benefit from being reared at a warmer temperature. Fish from the Sebago population had faster burst speeds and also exhibited plasticity in preferred temperature. Plasticity in preferred temperature allows the population to find suitable thermal habitats in streams that have variable temperatures through the year, and may experience extreme heat events in the summer. This population may be the more promising population for reintroduction efforts because they displayed this plasticity.

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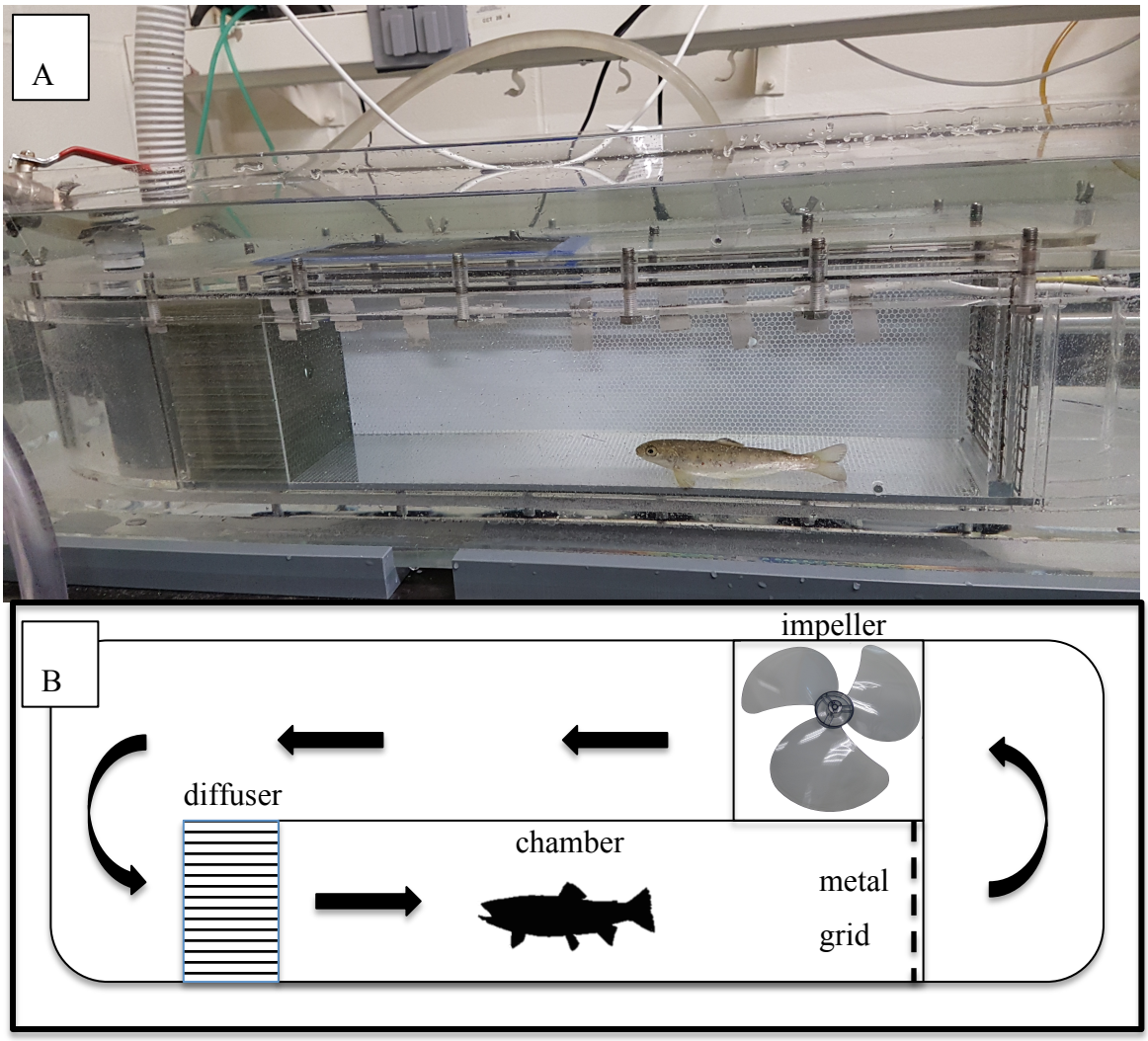
Appendices

Appendix A. The randomized order of water temperatures (°C) used for burst speed trials of Atlantic salmon. Blocks were used to describe fish that underwent trials at the same time through the same order of temperatures, and also correspond to order of calendar dates (block 1 fish performed trials months before block 15).

Block														
1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
17	13	17	13	25	19	25	19	13	17	23	25	17	15	25
19	25	11	25	13	23	19	11	23	11	17	15	11	23	13
15	17	19	17	17	17	13	15	21	19	25	21	13	13	23
13	21	15	19	23	25	21	25	11	13	13	13	21	11	11
21	11	23	15	21	21	23	17	19	23	21	11	15	17	21
23	15	21	23	19	11	15	23	15	15	19	19	25	21	19
11	23	13	21	11	15	11	13	25	25	15	17	19	19	17
25	19	25	11	15	13	17	21	17	21	11	23	23	25	15

Appendix B: A) A photo of an Atlantic salmon swimming in the swim flume. B) A schematic of the swim flume showing the impeller, diffuser, chamber and metal grid. The arrows represent laminar flow.

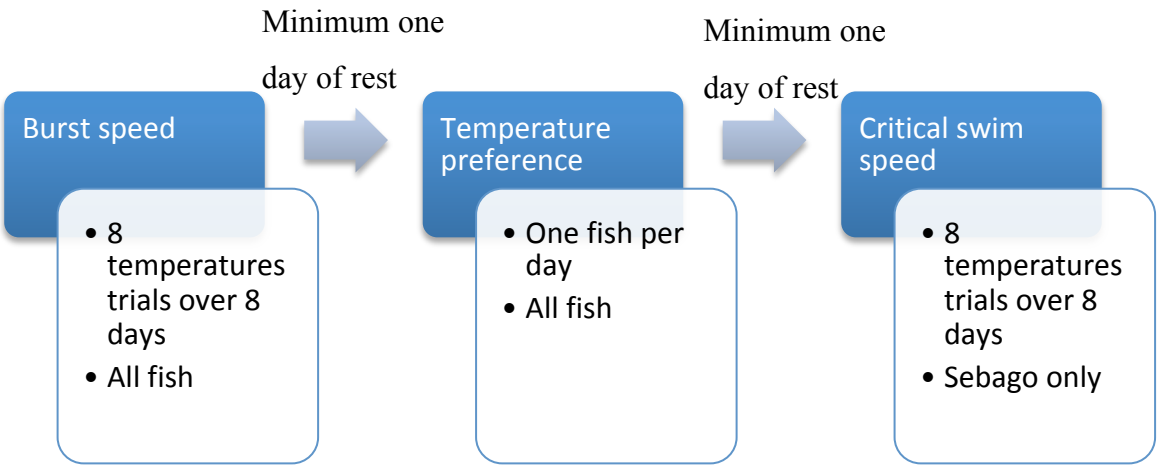


Appendix C: The semi-randomized order of water temperatures (°C) used for critical swim speed trials of Atlantic salmon. Groups were used to describe fish that underwent trials at the same time through the same order of temperatures, and also correspond to order of calendar dates (block 1 fish performed trials before block 3). Fish died during group 1 at the highest test temperatures, so subsequent groups ended in the highest test temperatures of 23 and 25.

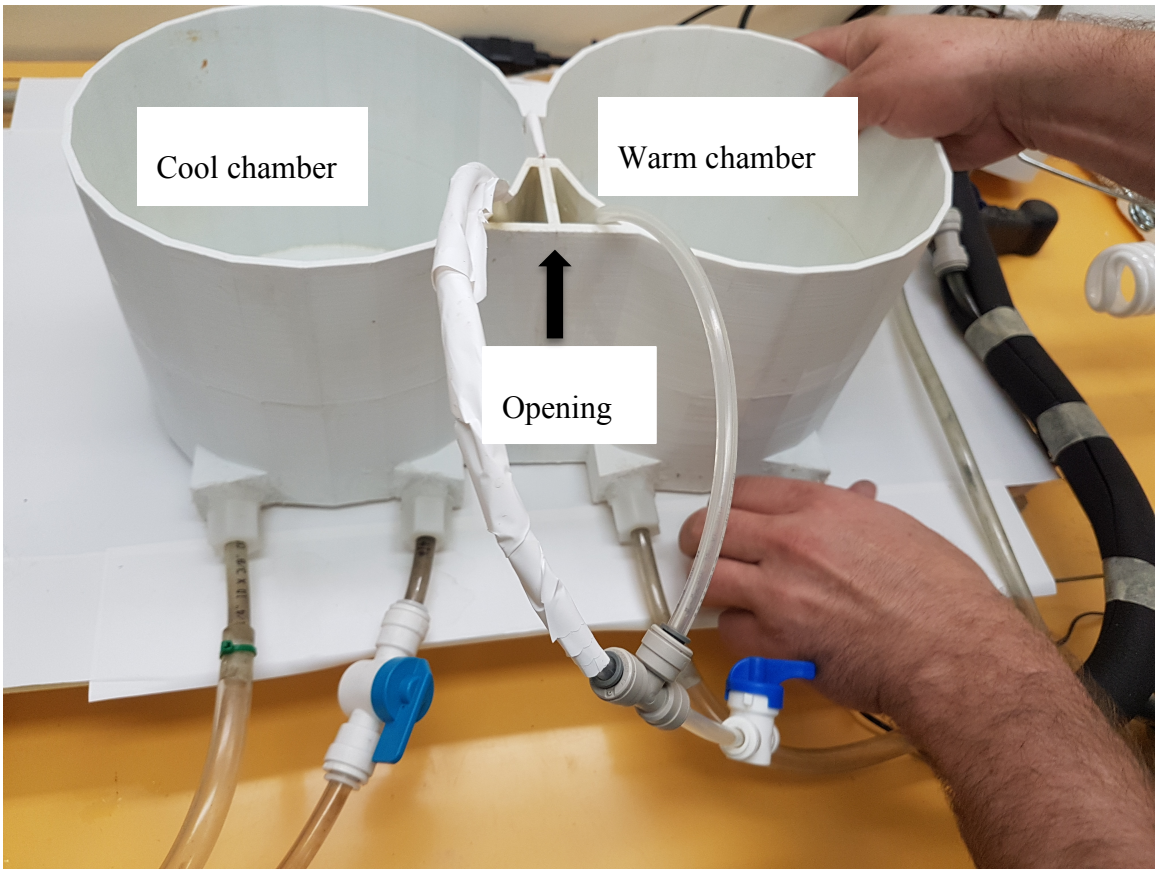
Group		
1	2	3
11	19	17
21	11	19
13	21	11
15	13	21
19	15	13
25	17	15
23	23	23
17	19*	25

* Group 2 was subjected to 19°C during the last day of trials due to an error. Therefore, this data was omitted, and the first day of trials at 19°C was used instead. Fish in group 2 were never tested at 25°C.

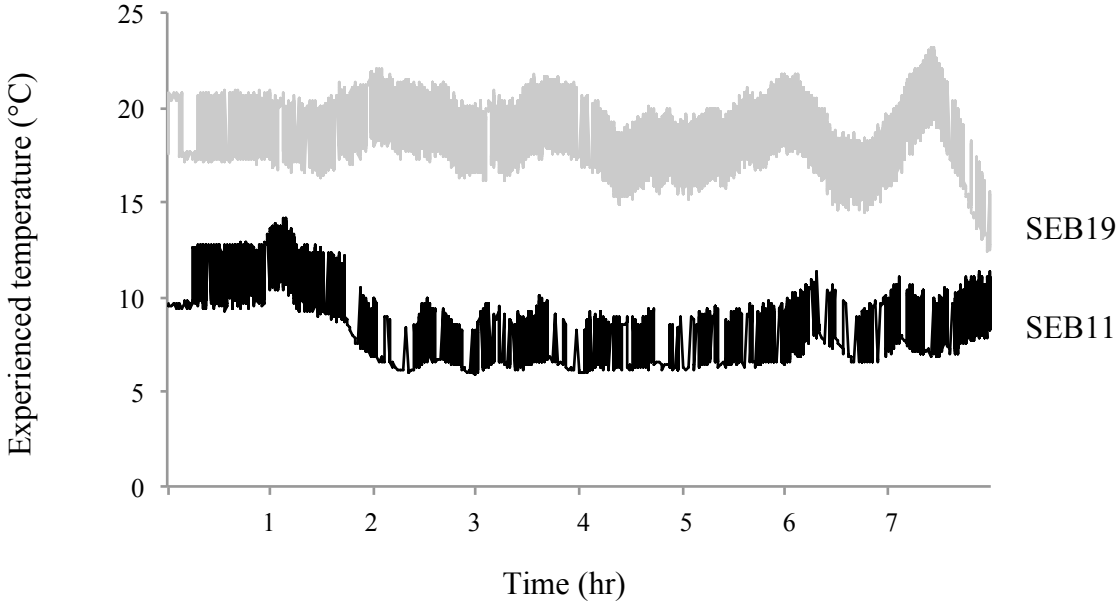
Appendix D: Flow chart of the sequence of metrics that a single juvenile Atlantic salmon underwent. Burst speed trials were completed over 8 days. A minimum of one day of rest was given before temperature preference trials were start. Temperature preference trials were performed on each fish individually over the next week. Then a subset of fish from the Sebago population underwent critical swim speed trials.



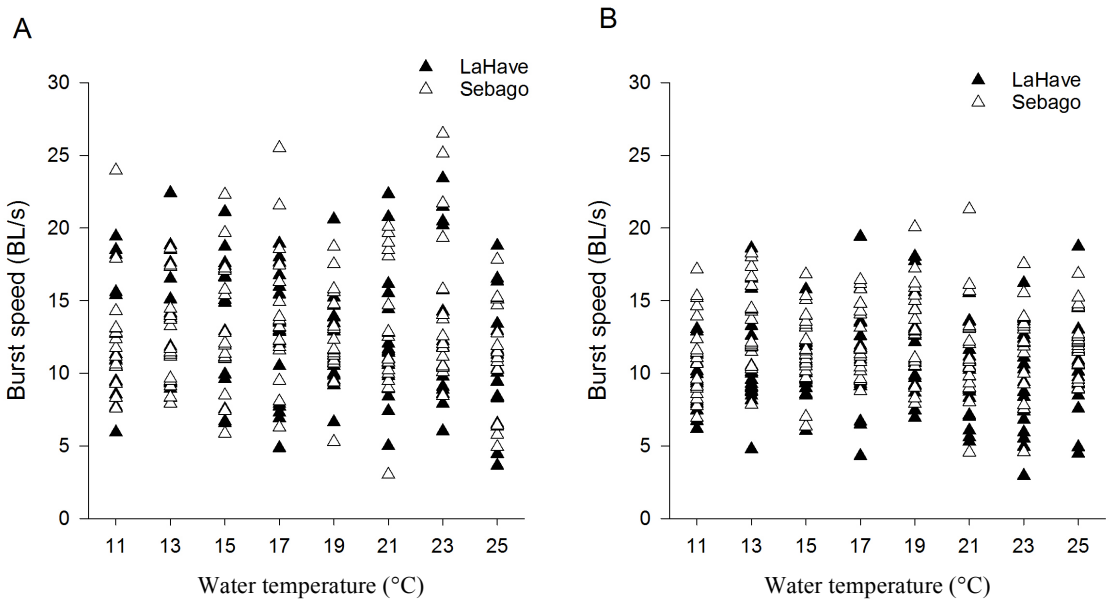
Appendix E. A photo of the shuttlebox showing the two chambers and the opening between them.



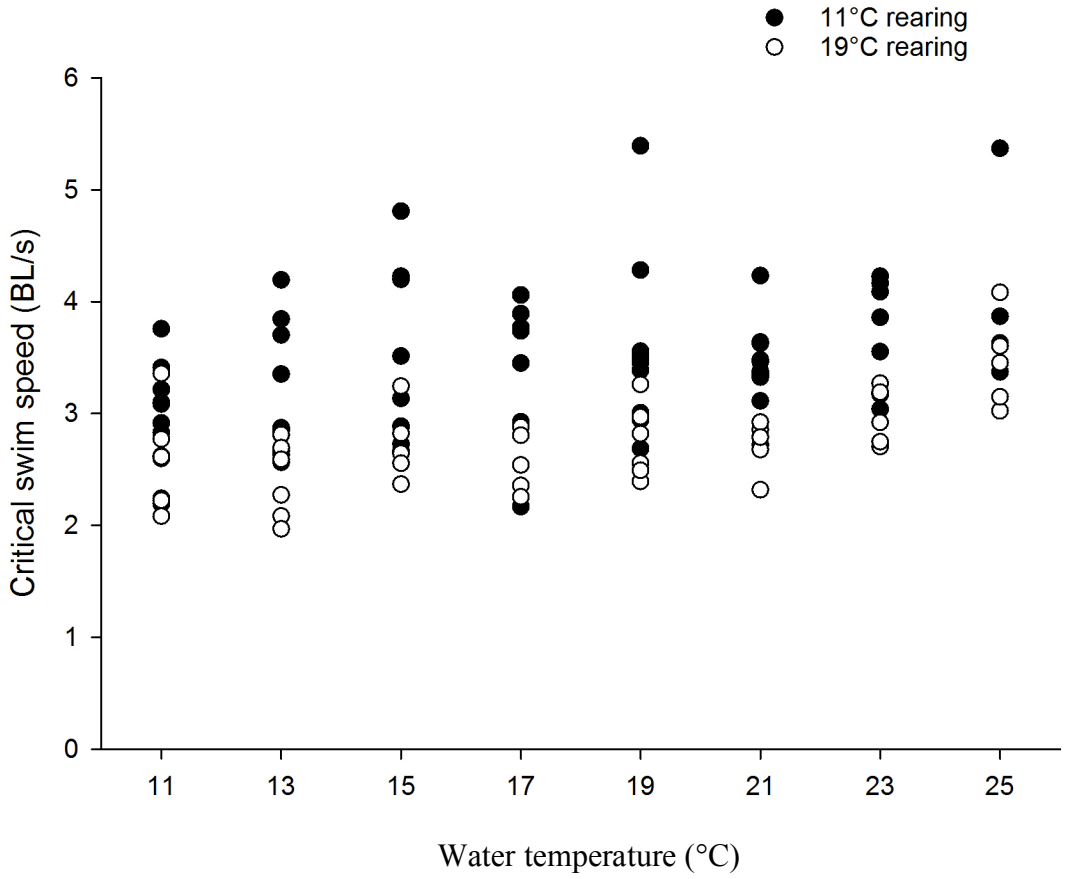
Appendix F. Examples of raw shuttlebox data for an Atlantic salmon from the Sebago population reared at 19°C (grey) or reared at 11°C (black). Experienced temperature is the temperature the fish was exposed to (depending on what chamber of the shuttlebox was occupied) and was recorded every second throughout trials.



Appendix G: Burst speed (BL/s) as a function of water temperature for juvenile Atlantic salmon (*Salmo salar*) reared at (A) 11°C or (B) 19°C.



Appendix H: Critical swim speed (BL/s) as a function of water temperature for juvenile Atlantic salmon (*Salmo salar*) from the Sebago population.



Appendix I. Animal Use Protocol

AUP Number: 2010-214
PI Name: Neff, Bryan
AUP Title: Behavioural and molecular ecology of fishes
Approval Date: 06/09/2014

Curriculum Vitae

Nicole Zathey

Post-Secondary Education and Degrees

Masters of Science in Biology, University of Western Ontario (September 2016 – Present)

Honours Bachelors of Life Science, McMaster University (September 2011 – April 2016)

Honours and Awards

Western Biology Travel Award, University of Western Ontario, Spring 2018

Great Lakes Fishery Commission Travel Award, Great Lakes Fishery Commission, 2017

2nd Best Oral Presentation, McMaster Interdisciplinary Symposium, McMaster, 2016

Best Poster, Ontario Biology Day, Ryerson University, 2016

Honour Award Level 2, McMaster University, 2011-2012

Work Experience

Teaching Assistant, University of Western Ontario, London, ON, 2016 – 2018

Field Research Assistant, McMaster University, Hamilton, ON, 2015

Teaching Assistant, McMaster University, Hamilton, ON, 2015

Laboratory Research Assistant, McMaster University, Hamilton, ON, 2014-2015

Conference Presentations

Zathey, N., Tattersall, G. J., Neff, B. (2018) Swim performance and temperature preference of Atlantic salmon. Ecology and Evolutionary Ethology of Fishes. Montreal, QC, Canada. [Oral]

Zathey, N., Tattersall, G. J., Neff, B. (2018) Some like it hot: Thermal performance and swim preference of Atlantic salmon. Canadian Society of Zoology Meeting. St. John's, NL, Canada. [Oral]

Zathey, N. & Neff, B. (2017) Thermal ecology of Atlantic salmon. International Association of Great Lakes Research. Detroit, MI, United States. [Poster]

Zathey, N. & Chow-Fraser, P. (2016) Factors affecting northern pike nursery habitat suitability in northern Georgian Bay. McMaster Interdisciplinary research symposium. Hamilton, ON, Canada. [Oral]

Zathey, N. & Chow-Fraser, P. (2016) Factors affecting northern pike nursery habitat suitability in northern Georgian Bay. Ontario Biology Day. Toronto, ON, Canada. [Poster]